植物研究雑誌
J. Jpn. Bot.
74: 236–250 (1999)

Anatomy of Nodal Regions and Leaves in *Hedysarum* and Related Genera (Leguminosae)

Byoung-Hee CHOI[a], Tomoyuki NEMOTO[b,*] and Hiroyoshi OHASHI[b]

[a]Department of Biology, Inha University, Incheon, 402-751 KOREA;
[b]Biological Institute, Graduate School of Science, Tohoku University, Sendai, 980-8578 JAPAN
*Current address: Department of Basic Sciences, Faculty of Science and Engineering, Ishinomaki Senshu University, Ishinomaki, 986-8580 JAPAN

(Received on February 3, 1999)

Vascular system from the stem to petiole and anatomical and epidermal features of the leaf were examined in *Corethrodendron*, *Hedysarum*, *Stracheya* and *Taverniera*. Two types of the vascular system were observed at the node: trilacunar type and multilacunar type. The trilacunar type was found in subgenera Gamotion and Hedysarum of genus *Hedysarum* and genus *Stracheya*. It is the commonest type among the taxa examined. On the other hand, the multilacunar type was restricted in subgenus Heteroloma of genus *Hedysarum* and genus *Taverniera*. The vascular systems at the node of stem and at the base of petiole in the taxa examined are not associated with number of leaflets and length of internodes which have been regarded as important diagnostic characters in classification for these four genera. The petioles have bundles fused altogether at least once at the base in all the species examined except *Hedysarun spinosissimum* of subgen. Hedysarum which has open (free) bundle system. Although the species of subgen. Hedysarum have unique stipules, no specific vascular systems were observed. The bundle sheath extention of lateral vein of leaflets was observed only in sect. Gamotion of subgen. Gamotion of *Hedysarum*. Also, this section differs from other sections of the subgenus by lacking a distinctly developed cuticular membrane. *Stracheya* is similar to subgen. Gamotion of *Hedysarum* in anatomical characters of the node and the leaf. Subgen. Heteroloma of *Hedysarum* is closer to genera *Corethrodendron* and *Taverniera* than other subgenera of *Hedysarum* in the characteristics of nodal anatomy, leaf traces and leaf epidermis.

Key words: leaf epidermis, petiole, Leguminosae, tribe Hedysarae, vascular system

Introduction

Hedysarum and its related genera belonging to the tribe Hedysareae of subfamily Papilionoideae in Leguminosae (Hutchinson 1964, Polhill 1981a) are distributed in temperate to boreal regions of Northern Hemisphere. *Hedysarum* is closely related to *Corethrodendron*, *Stracheya* and *Taverniera* in gross and pollen morphologies (Ohashi 1971, Choi 1988, Choi and Ohashi 1996), but has been distinguished from these genera by number of leaflets and shape of fruits. However, delimitation of these four genera is still controversial (Polhill 1981b, Thulin 1985, Choi 1988, Choi and Ohashi 1996). In order to clarify intergeneric relationships among *Hedysarum*, *Corethrodendron*, *Stracheya* and *Taverniera*, and infrageneric relationships in *Hedysarum*, we examined vascular systems at the nodal regions and petioles of leaves and anatomical and epidermal features of leaves in these genera. Although taxonomic significance of such studies in Leguminosae was already emphasized by Watari (1934), only a few anatomical studies on branching patterns of leaf traces at the base of petioles have been made in tribe Hedysareae. Vogelsberger (1893) studied anatomical features of leaves and stems on several species of Hedysareae. He found several types of stomata and leaf-veins and tannin in stems. Northstrom (1974) described anatomical features of the stem, leaflet and petiole together with flower, loment, seed and root in North American species of *Hedysarum*, but did not add taxonomic consideration. Leaf anatomy of several species of *Taverniera* and *Hedysarum* was made by Thulin (1985), but no significant differences between the two genera were found.

Vascular systems from the stem to petiole and anatomical features of the leaf epidermis are studied in this work, therefore, in order to find useful characteristics to clarify intergeneric relationships among *Hedysarum* and its related genera and the infrageneric relationships in genus *Hedysarum*.

Materials and Methods

Most of the materials examined in this study were obtained from herbarium specimens listed in Appendix 1. A few materials were obtained from fresh plants cultivated in the green house of Biological Institute, Tohoku University.

The materials from herbarium specimens were softened in boiling water for about 10 min. For the study of vascular systems of the nodal regions, sections were taken from the upper internode of stem through the node to the petiolar base, and for the vascular system of petiole, from the middle part of the petiole, that is, mid length between node and first leaflet pair. Only one nodal region with a petiolar base was used from one herbarium specimen for each species to examine the vascular system from the upper internode to the petiolar base, while leaves from one or several specimens were used for each species to examine the vascular pattern of the petiole. The material was frozen in liquid nitrogen in a foil boat, and then sectioned at a thickness of 15–20 μm using a freezing microtome in a cold box. The sections were adhered to slides by albumine and washed in distilled water at 70°C for about 20 min. The sections were stained with 1 % safranine, dehydrated in an ethanol series, cleared in xylol and mounted in Canada balsam. The serial sections of each sample were examined and drawn by a Zeiss-III photomicroscopy.

For the observations of cross sections and epidermal surfaces of leaflets, leaflets were collected from herbarium specimens and fixed by FAA at first. The cross sections of them were obtained by hand using a razor, dehydrated by an ethanol series, transferred to isoamyl acetate, dried in a critical point dryer, mounted on aluminum stubs with a silver paste, coated with gold, and then observed in a JEOL JSM 840 scanning electron microscopy (SEM). Some specimens were frozen in liquid nitrogen and observed with a SM-CRU 40 crio-system using the SEM.

Results

1. Vascular system at the node

Vascular systems at the node were examined in seven species of *Hedysarum*, which represent three subgenera and four sections, *Stracheya tibetica* and *Taverniera nummularia* (Appendix 1.1). Leaf traces were bent toward the base of leaf petiole from the vascular cylinder in the stem. In the transverse sections of the nodal regions trilacunar or multilacunar nodes were observed (Table 1).

Table 1. Leaf and nodal anatomical characters investigated in the present study of *Hedysarum* and related genera

	Number of leaflet	Leaf gap	Stipule	Lateral vein of leaflet	Cuticle on leaflet	Vascular type of petiole*1
Corethrodendron	more than 5	NI	sheathing	obscure	developed	F
Hedysarum						
Subgen. Gamotion						
Sect. Crinifera	more than 5	NI	sheathing	obscure	distinctly developed	C & D
Sect. Gamotion	more than 5	3	sheathing	conspicuous*2	developed	C & D
Sect. Membranacea	more than 5	3	sheathing	obscure	developed	F
Sect. Multicaulia	more than 5	3	sheathing	obscure	distinctly developed	C
Sect. Subacaulia	(1–3) or more than 5	3	sheathing	obscure	distinctly developed	B & C
Subgen. Hedysarum	more than 5	3	free, adnate with petiole	obscure	developed	A & E
Subgen. Heteroloma	more than 5	5	sheathing	obscure	developed	F
Stracheya	more than 5	3	sheathing	obscure	developed	E
Taverniera	1–3	3+1	sheathing	obscure	developed	E

NI, not investigated; *1, see text for the explanation; *2, with bundle-sheath extention.

1) Trilacunar node: Three leaf traces are coming out from the vascular cylinder of the stem leaving three gaps. This type of the node, trilacunar node, is most common in the species examined, and observed in subgenera Gamotion and Hedysarum of genus *Hedysarum* (Figs. 1A, 2A, 3A, 5) and *Stracheya tibetica* (Fig. 6).

2) Multilacunar node: More than three leaf traces are coming out from the vascular cylinder leaving each gap, and this is multilacunar type. Two forms were found with respect to the number of leaf traces in this type. One has five leaf traces, each of which is almost equal in size and not fused with each other before entering into the petiole. This form was observed only in the species of subgenus Heteroloma of genus *Hedysarum* (Fig. 4A). The other has four leaf traces (Fig. 7A), one of which is significantly smaller in size than others. We call it an 'additional trace' in the present study ('at' in Fig. 7A). This additional trace fused with one of the lateral bundles before entering into the petiole (Fig. 7B). This form was observed only in *Taverniera nummularia* (Fig. 7A, B).

2. Vascular system from the node to petiolar base

General features: The vascular system between the node and the base of the peti-

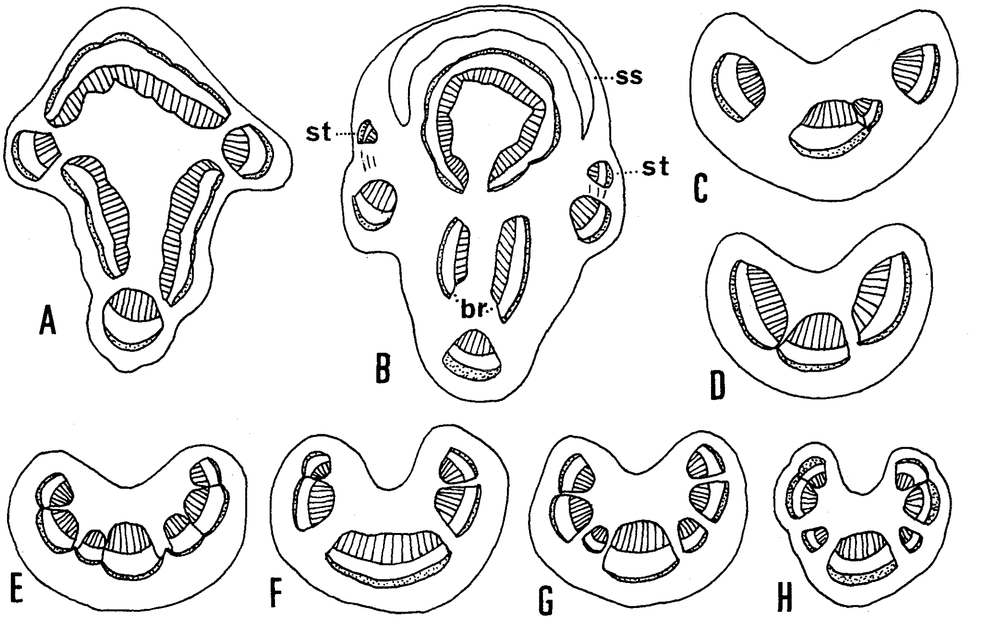


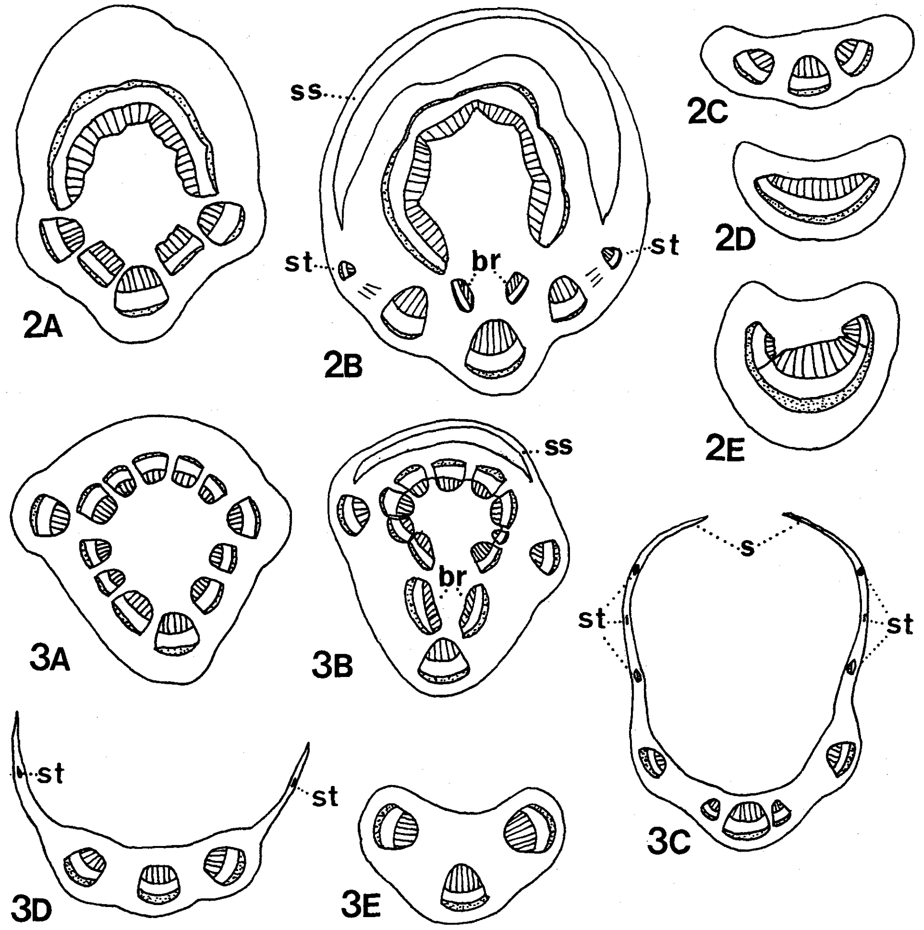
Fig. 1. Diagrams of vascular bundles from nodal region to petiole in *Hedysarum gmelini*. A, B. Nodal region from proximal to distal parts. C-G. Petiolar base from proximal to distal parts. H. Middle part of petiole. Hatched and dotted areas show xylem and sclerenchyma, respectively. br, branch trace; ss, sheathing stipule; st, stipular bundle.

ole was examined in six species (Appendix 1.1). At the internode of the stem, vascular bundles form a continuous ring in all species examined. At the node, leaf traces are branched off from the vascular cylinder of the stem leaving each gap (Figs. 1A, 2A, 3A, 4A, 5, 6, 7A). Two branch traces are branched off from the vascular cylinder of the stem at the both sides of the median gap. In the species having the trilacunar type of node, two lateral gaps are closed to form an arc with an opening behind two branch traces ('br' in Figs. 1B, 2B, 3B). The stipular bundle is branched off from each of two lateral traces, and extends to the sheathing stipules surrounding the stem ('st' in Figs. 1B, 2B, 3C, 7B). The vascular bundles of the stem are fused to form a ring again above the node. On the other hand, the leaf traces run separately and then fuse or connect with each other before entering into the base of petiole.

1) *Hedysarum gmelini* (subgen. Gamotion sect. Multicaulia: Figs. 1A-H): Three leaf traces branched off from the vascular cylinder of the stem change their forms from those fused altogether to those segmented into small bundles or those connected with an arc at the petiolar base even within the same petiole (Fig. 1C-G).

2) *Hedysarum monophyllum* (subgen. Gamotion sect. Subacaulia: Fig. 2A-E): Among three leaf traces branched off, two lateral leaf traces are smaller in size than the median trace (Fig. 2B). The three leaf traces separately enter into the petiolar base (Fig. 2C) and then completely fuse into a bundle of semilunar shape (Fig. 2D).

3) *Hedysarum spinosissimum* (subgen. Hedysarum: Fig. 3A-E): In the whole petiole, three leaf traces are completely separated, that is, forming an open system. In the

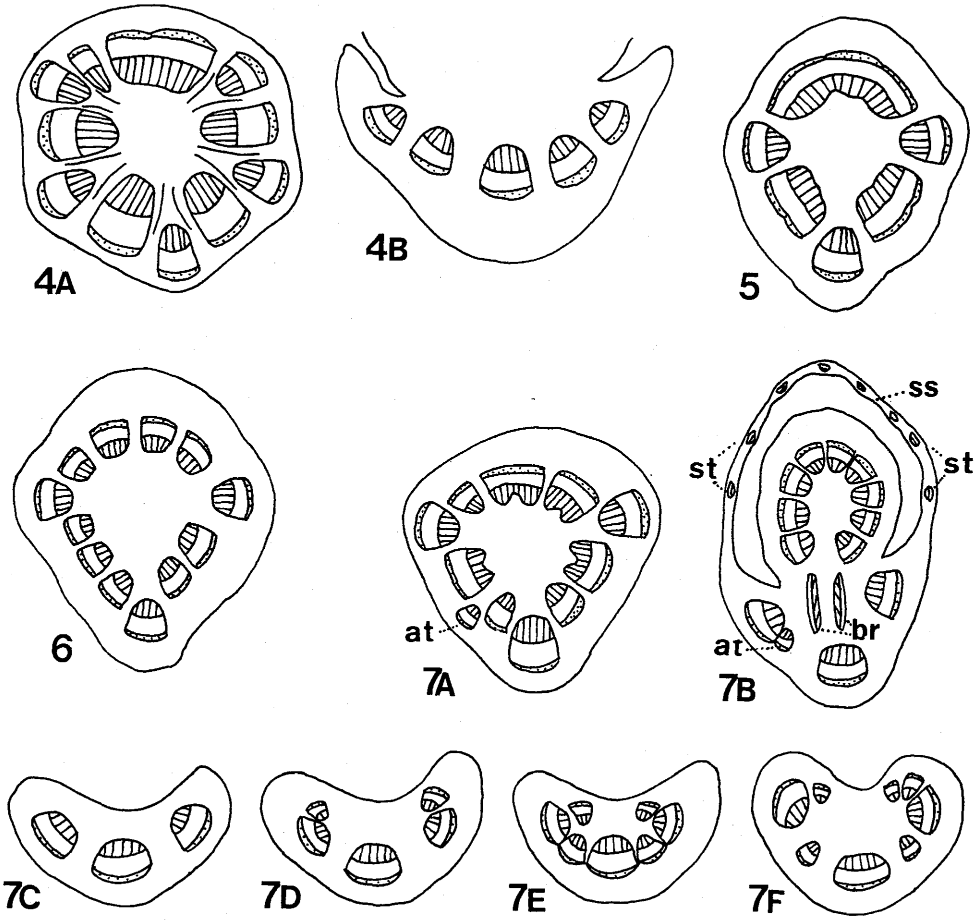


Figs. 2–3. Diagrams of vascular bundles from nodal region to petiole in *Hedysarum monophyllum* (2A–2E) and *H. spinosissimum* (3A–3E). A, B. Nodal region from proximal to diatal parts. C, D. Petiolar base from proximal to distal parts. E. Middle part of petiole. Hatched and dotted areas show xylem and sclerenchyma, respectively. br, branch trace; s, stipule adnate with petiolar base; ss, sheathing part of stipule; st, stipular bundle.

petiolar base, the median bundle is segmented into three parts first (Fig. 3C) and then they are fused into one bundle again later (Fig. 3D). Two lateral bundles are segmented and fused again like the median bundle (without illustration). Although this species has unique stipules basally adnate with the petiole (Fig. 3C, D), stipular bundles (st) are branched off from lateral traces like other species with sheathing stipules and segmented into three traces (Fig. 3C).

All species comprising subgen. Hedysarum are annual herbs except *H. coronarium* of a perennial herb. In this species, however, the pattern of vasculature at the petiolar base was not similar to that of *H. spinosissimum*, but to that of *H. gmelini* (subgenus Gamotion; Fig. 1) in having almost fused bundles.

4) *Hedysarum fruticosum* subsp. *mongolicum* (subgen. Heteroloma: Fig. 4A,



Figs. 4–7. Diagrams of vascular bundles of nodal region and petiole in *Hedysarum*, *Stracheya* and *Taverniera*. 4. *H. fruticosum* subsp. *mongolicum*: 4A, Nodal region; 4B, Petiolar base. 5. Nodal region of *H. vicioides* var. *japonicum*. 6. Nodal region of *S. tibetica*. 7. *T. nummularia*: 7A–7B, Nodal region from proximal to distal parts; 7C–7E, Petiolar base from proximal to distal parts; 7F, Middle part of petiole. Hatched and dotted areas show xylem and sclerenchyma, respectively. br, branch trace; ss, sheathing stipule; st, stipular bundle.

B): Five leaf traces come out from the vascular cylinder of the stem (Fig. 4A). These five leaf traces separately enter into the petiole (Fig. 4B).

5) *Taverniera nummularia* (Fig. 7A-F): Among the four leaf traces, the additional trace (at) is fused with the adjacent lateral trace at the node, and then three traces separately enter into the petiole (Fig. 7B). The vascular system at the petiolar base were composed of a median and two lateral bundles (Fig. 7C). The lateral bundles are segmented and then connate to each other later between the basal and middle parts of the petiole (Fig. 7D, E). The connate bundles are, however, separated again at the middle part of the petiole (Fig. 7F).

3. Vascular system in the middle part of petiole

Cross sections of the middle part of petiole, that is, mid length between the petiolar

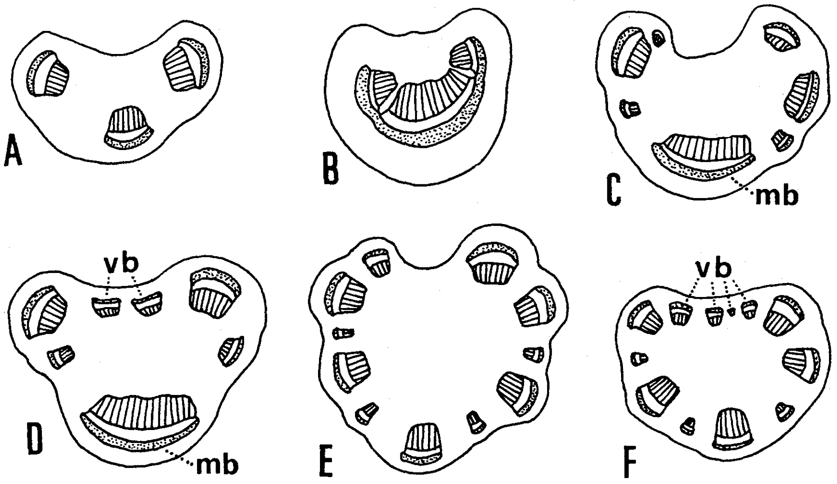


Fig. 8. Diagrams showing six types of petiolar vascular patterns in *Hedysarum* and related genera. Hatched and dotted areas show xylem and sclerenchyma, respectively. mb, median bundle; vb, ventral bundle. See text for explanation.

base and the first leaflet pair, were observed in 17 species of *Hedysarum*, *Corethrodendron scoparium*, *Stracheya tibetica* and *Taverniera nummularia* (Appendix 1.2). In this study, the vascular system of petiole was classified into six types according to fused or free vascular bundles and presence or absence of median and ventral bundles (Fig. 8, Table 1).

Type A: Vascular system formed by three separated bundles of almost equal size–*Hedysarum spinosissimum* (subgen. Hedysarum).

Type B: Vascular system formed by three bundles almost fused in an arc–*Hedysarum monophyllum* (subgen. Gamotion sect. Subacaulia).

Type C: Vascular system of 'U'-shaped or arced, composed of a large median bundle (mb) and several small lateral segments–*Hedysarum macranthum* (subgen. Gamotion sect. Crinifera), *H. hedysaroides*, *H. inundatum*, *H. sikkimense*, and *H. vicioides* var. *japonicum* (subgen. Gamotion sect. Gamotion), *H. brachypterum* and *H. gmelini* (subgen. Gamotion sect. Multicaulia), and *H. ferganense* (subgen. Gamotion sect. Subacaulia).

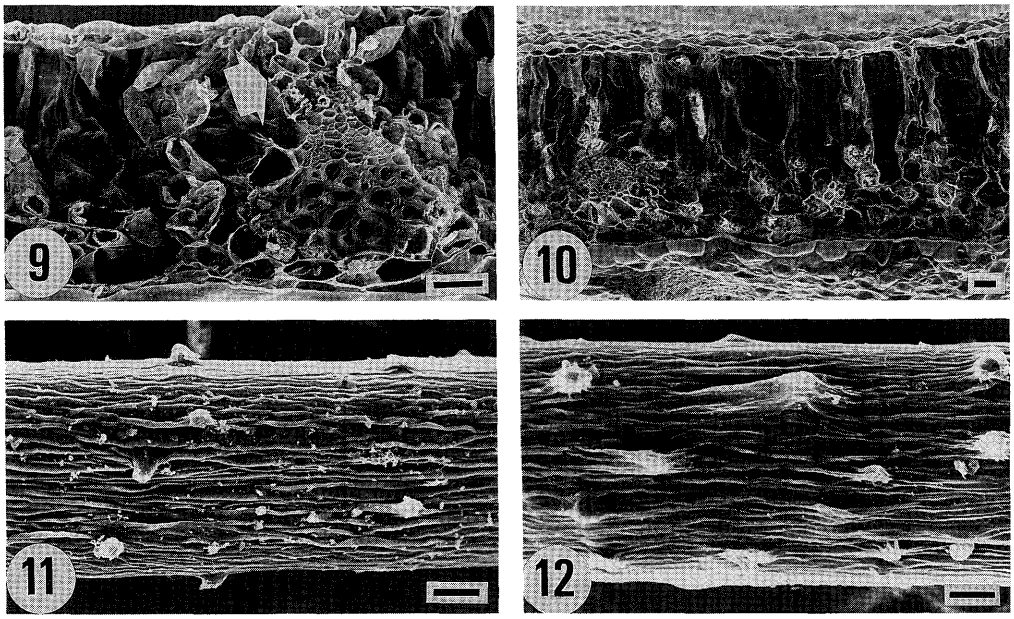
Type D: Vascular system with the ventral bundles (vb) in addition to the bundles of Type C–*Hedysarum micropterum* (subgen. Gamotion sect. Crinifera), and *H. falconeri* (subgen. Gamotion sect. Gamotion).

Type E: Vascular system of 'U'-shaped, composed of segmented bundles without forming a large median bundle–*Hedysarum coronarium* and *H. glomeratum* (subgen. Hedysarum), *Stracheya tibetica*, *Taverniera nummularia*.

Type F: Vascular system with the ventral bundles in addition to the bundles of type E–*Corethrodendron scoparium*, *Hedysarum fruticosum* subsp. *mongolicum* and *H. multijugum* (subgen. Heteroloma), and *H. membranaceum* (subgen. Gamotion sect. Membranacea).

4. Bundle-sheath extention in the leaflet

The bundle-sheath extention of leaflet blade was observed in 36 species of *Hedysarum* and related genera such as *Corethrodendron*, *Stracheya* and *Taverniera*



Figs. 9–12. Cross-sections of lateral veins in leaf blades (9, 10) and surface views of trichome on abaxial leaf surface (11, 12) of *Hedysarum*. 9. *H. vicioides* var. *japonicum*, arrow indicating bundle-sheath extension. 10. *H. coronarium*, showing no bundle-sheath extention. 11. *H. ferganense*. 12. *H. coronarium*. Scale bars = 50 μm (9, 10), 10 μm (11, 12).

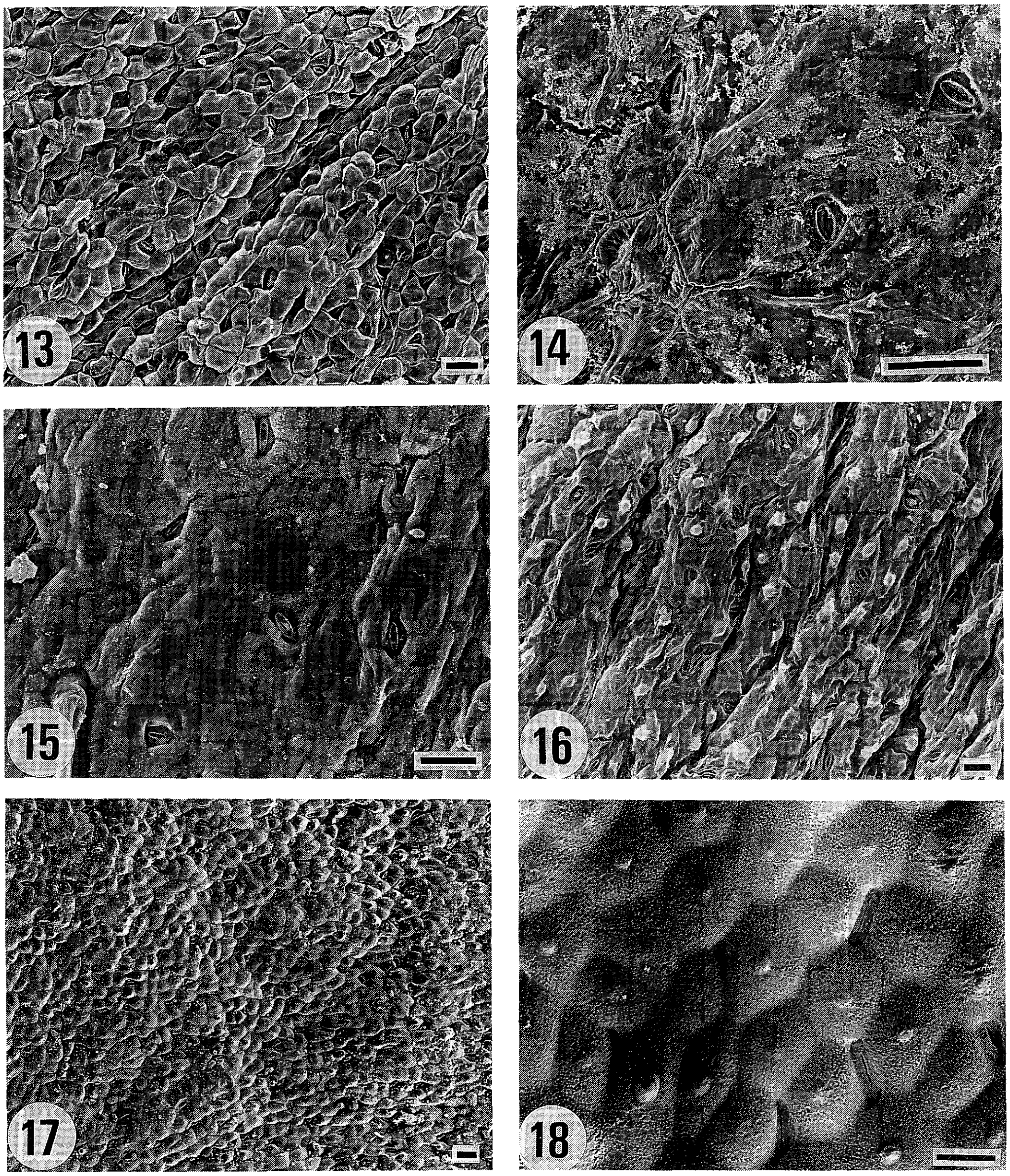
(Appendix 1.3).

In the cross section of leaflet blade, the bundle-sheath extention which is a plate of ground tissue extending from a bundle sheath to the epidermis in a leaf (Wylie 1952, Esau 1977) was observed along the lateral veins of leaflets only in the species of sect. Gamotion of *Hedysarum* (Fig. 9). Because the cells of the bundle-sheath extention reach to the epidermis, the epidermal cells along the lateral veins are different in shape from those of other parts (Fig. 13). Therefore the lateral veins become conspicuous from surface view in the species with bundle-sheath extention (Table 1), although the conspicuousness of the lateral vein was variable among individuals in *H. pseudoastragalus* and *H. sikkimense* in sect. Gamotion. On the contrary, the lateral veins are obscure in the species without those (Figs. 17, 19).

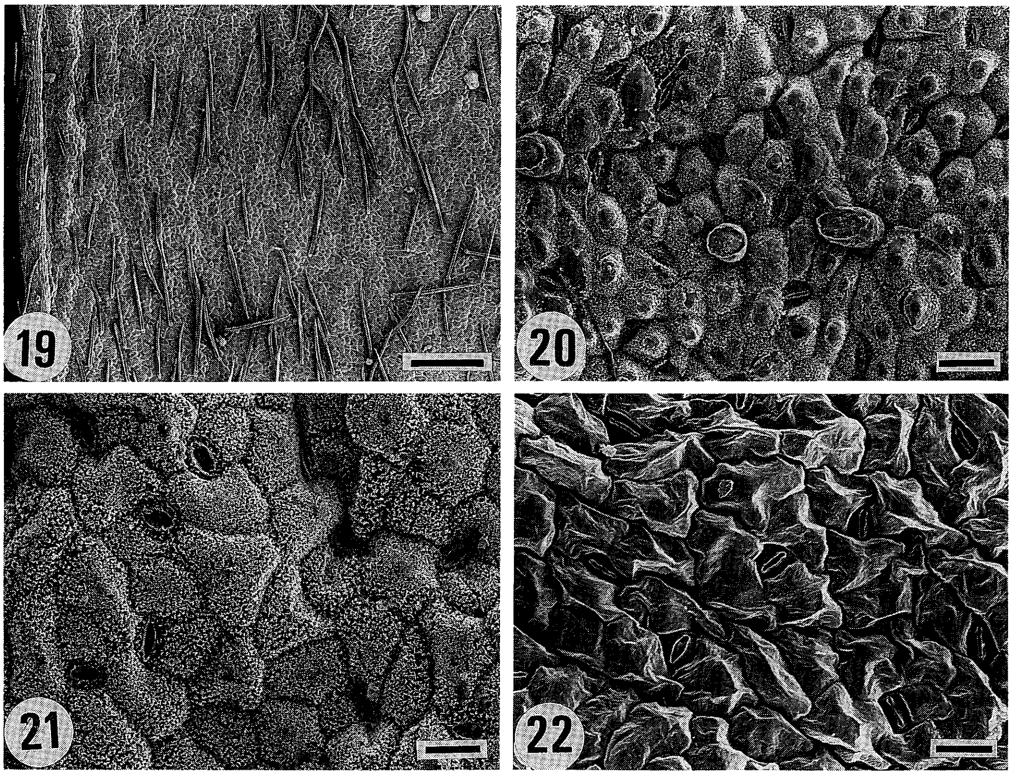
The leaflet blade is distinctly thinner in sect. Gamotion than other infrageneric groups of *Hedysarum* and other genera. Therefore, the presence of bundle-sheath extention is likely to associate with the thickness of leaflet blade.

5. Epidermis of the leaflet

Hairs on the leaflet surface were similar in morphology among all 36 species observed in the present study (Appendix 1.3). Striate sculpture of cuticles and protuberances were observed on the surface of hairs (Figs. 11, 12). The hairs on the leaf surface showed variation in distribution among infra- or intergeneric groups. The epidermis of leaflets was densely covered with hairs in sections. Crinifera, Multicaulia and Subacaulia of *Hedysarum* subgen. Gamotion, while it was glabrous or slightly pubescent in sect. Gamotion of subgen.



Figs. 13–18. Adaxial surface views of leaflets of *Hedysarum*. 13. *H. sikkimense* var. *megalanthum*, showing conspicuous lateral vein from surface view. 14. *H. micropterum*, showing the shape of each epidermal cell hardly distinguished. 15. *H. subglabrum*, showing the shape of each epidermal cell hardly distinguished. 16. *H. lehmannianum*, showing the shape of each epidermal cell hardly distinguished. 17. *H. membranaceum*, showing obscure lateral veins from surface view. 18. *H. coronarium*, observed with SM-CRU crio-system, showing the shape of each epidermal cell well distinguished. Scale bars = 50 μm.



Figs. 19–22. Adaxial surface views of leaflets of *Hedysarum* and related genera. 19. *H. fruticosum* subsp. *mongolicum*, showing obscure lateral veins from surface view. 20. *Corethrodendron scoparium*, showing the shape of each epidermal cell well distinguished. 21. *Taverniera nummularia*, showing the shape of each epidermal cell well distinguished. 22. *Stracheya tibetica*, showing the shape of each epidermal cell well distinguished. Scale bars = 500 μm (19), 50 μm (20–22).

Gamotion and subgenera Hedysarum and Heteroloma of *Hedysarum*, *Corethrodendron*, *Stracheya* and the most species of *Taverniera*.

Cuticular membranes in the leaflet epidermis were well-developed in such groups as sections Crinifera, Multicaulia and Subacaulia of *Hedysarum* (Figs. 14–16, Table 1). Because the cuticular membranes were well-developed even in the area between the epidermal cell walls (cuticular flange; Stace 1965), the shape of each epidermal cell of those species could not be distinguished from surface view by SEM. On the contrary, it was cleary distinguished from surface view in other groups (Figs. 13, 17–22).

Discussion

Three nodal types, unilacunar, trilacunar, and mutilacunar types, were recorded by Watari (1934) in Leguminosae. The trilacunar type was most common in the family, but the unilacunar type was only recorded in some species in tribe Genisteae, and the multilacunar type was sporadically found in subfamilies Caesalpinioideae and Papilionoideae (Watari 1934). The trilacunar type was inferred to be the more primitive type in Leguminosae (Polhill 1981a). This type is most common in *Hedysarum* and related genera examined in this study, while the multilacunar type was observed in *Taverniera nummularia* and *Hedysarum fruticosum* subsp. *mongolicum* of subgen. Heteroloma.

Watari (1934) emphasized that "the petiolar base is one of the most important regions in the vascular course of foliar organs of Leguminosae." He classified branching patterns of the vascular bundles at the petiolar bases into three types based on the number of leaf traces and whether the traces are fused or free. In the present study, three leaf traces were fused altogether at least once in the most species, whereas those were completely separated or free in *H. spinosissimum* of subgen. Hedysarum.

Petiolar vascular systems in *Hedysarum* and related genera were divided into six types according to the arrangement or segmentation of vascular bundles and presence or absence of large median bundles and ventral bundles. However, the pattern of the petiolar bundles shows variation even in a species in some sections and subgenera of *Hedysarum* (Table 1). On the other hand, the scattered bundle pattern with ventral bundles in the petiole, or Type F, was observed only in shrubby species such as sect. Membranacea and subgen. Heteroloma of *Hedysarum* and *Corethrodendron*. The vascular system of the petiole was shown not to be associated with any of the number of leaf trace, the branching pattern of leaf traces at the petiolar base, and the number of leaflets.

Genus *Stracheya*, a monotypic genus, has been distinguished from *Hedysarum* in having fruits with prickles. However, the genus is very similar to sections Crinifera, Multicaulia and Subacaulia of genus *Hedysarum* subgen. Gamotion in all anatomical characters examined except the vascular system of petiole and the development of the cuticular membranes in leaf epidermal cell wall (Table 1). This result agrees with pollen morphology (Choi and Ohashi 1996).

Genus *Taverniera* is not clearly distinguished from genus *Hedysarum* (Polhill 1981b, Thulin 1985). The diagnostic character separating these two genera is the number of leaflets (Polhill 1981b), that is, 1–3-foliolate leaves in *Taverniera* against usually more than 3-foliolate in *Hedysarum*. Although *H. monophyllum* and *T. nummularia* commonly have unifoliolate leaves, the vascular systems of the nodal region and the petiole were apparently different between these two species (Figs. 2, 7). Therefore, the number of leaflets is considered not to correspond with the anatomical characters such as the vascular systems in the nodal region and the petiole. On the other hand, *Taverniera* has been inferred to be closely related with the species of *Hedysarum* subgen. Heteroloma in gross morphology (Polhill 1981b, Thulin 1985, Choi 1988) and pollen morphology (Choi and Ohashi 1996). The evidence from the nodal anatomy in having the multilacunar type also supports the close relationship between them. *Corethrodendron scoparium*, a monotypic species of the genus, has been treated as a species of *Hedysarum* subgen. Heteroloma (Fedtschenko 1902, Polhill 1981b), and the species is more related to subgen. Heteroloma and genus *Taverniera* in pollen morphology (Choi and Ohashi 1996). The similarity in the features of leaflet surface between *Hedysarum* subgen. Heteroloma, *Taverniera*, and *Corethrodendron* is also consistent with their closer relationships.

Species of subgen. Hedysarum have stipules basally adnate with petiole (Figs. 3C, D). This feature is one of the taxonomic characteristics distinguishing the subgenus from other subgenera of *Hedysarum* (Basiner 1845, Thulin 1985). However, the branching pattern of vascular bundles supplied to the stipules in subgen. Hedysarum is similar to those in other subgenera with sheathing stipules. *Hedysarum spinosissimum* of subgen. Hedysarum has an open vascular system at the petiolar base, while *H. coronarium* of the same subgenus has a fused vascular system like species of other subgenera. Therefore, taxonomic implications of the vascular system at the petiolar base are uncertain in this subgenus until more species will be investigated.

Within subgen. Gamotion, sect. Membranacea has been distinguished from other four sections Crinifera, Gamotion, Multicaulia, and Subacaulia in having shrubby habit and fruits with wide margins (Fedtschenko 1902). Moreover, sect. Membranacea is not similar in pollen morphology to the latter sections, but rather to subgen. Heteroloma (Choi and Ohashi 1996). The present study also showed the similarity between sect. Membranacea and subgen. Heteroloma in the vascular system of the petiole and in the characteristics of leaves such as hairs, cuticular membranes and leaf blade thickness.

The taxonomic delimitation among four sections Crinifera, Gamotion, Multicaulia, and Subacaulia of *Hedysarum* subgen. Gamotion are obscure (Choi 1988). These four sections are also difficult to distinguish from each other in vascular systems in their nodes and petioles. However, sect. Gamotion is clearly different from others in having leaflet lateral veins with bundle-sheath extention, thin leaflet blade, and leaflet surface covered with less-developed cuticular membrane and without dense hairs. The tissues of the bundle-sheath extention are generally of most frequent occurrence in species with thin leaves, but least common in those with thick ones (Wylie 1952). This general feature is also applicable to subgen. Gamotion. On the other hand, sections Crinifera, Multicaulia and Subacaulia of subgen. Gamotion resemble each other in well-developed cuticular membrane and dense hairs on the leaflet surface. Although sect. Subacaulia is distinguished from others by shortened internode of stem (Fedtschenko 1902), this character does not correlate with any special anatomical structures of nodes and leaves.

We are grateful to the curators of BM, E, PE, and TI for the loan of specimens and/or permission to collect plant materials from the specimens. This work was supported in part by a Grant-in-Aid for Korea-Japan Cooperative Science Program (to B. H. Choi) from the Korea Science and Engineering Foundation (966-0500-003-2) and by a Grant-in-Aid for Japan-Korea Cooperative Science Program (to H. Ohashi) from the Japan Society for the Promotion of Science.

References

Basiner T. 1845. Enumeratio monographica specierum generis *Hedysari*. Bull. Acad. St.-Pétersb. **6**: 305–315.

Choi B. H. 1988. A taxonomic study of the genus *Hedysarum* and its allied genera (Leguminosae). Ph.D. thesis, Faculty of Science, Tohoku Univ., 111 pp. with 28 plates (in Japanese).

—— and Ohashi H. 1996. Pollen morphology and taxonomy of *Hedysarum* and its related genera of the tribe Hedysareae (Leguminosae-Papilionoideae). J. Jpn. Bot. **71**: 191–213.

Esau K. 1977. Anatomy of Seed Plants. 2nd ed. 550 pp. John Wiley and Sons, New York.

Fedtschenko B. A. 1902. The genus *Hedysarum*. Act. Hort. Petrop. **19**: 185–342 (in Russian).

Hutchinson J. 1964. Tribe Hedysareae. The Genera of Flowering Plants **1**: 466–469. Oxford University Press, London.

Northstrom T. E. 1974. The genus *Hedysarum* in North America. Ph.D. thesis, Brigham Young Univ., 187 pp.

Ohashi H. 1971. A taxonomic study of the tribe Coronillae (Leguminosae), with a special reference to pollen morphology. J. Fac. Sci. Univ. Tokyo, Sect. III (Botany) **11**: 25–92, pls. 1–10.

Polhill R. M. 1981a. Papilionoideae. *In*: Polhill R. M. and Raven P. H. (eds.), Advances in Legume Systematics **1**: 191–208. Royal Botanic Gardens, Kew.

—— 1981b. Hedysareae. *In*: Polhill R. M. and Raven P. H. (eds.), Advances in Legume Systematics **1**: 367–370. Royal Botanic Gardens, Kew.

Stace C. A. 1965. Cuticular studies as an aid to plant taxonomy. Bull. Br. Mus. Nat. Hist., Ser. E, **4**(1): 3–78.

Thulin M. 1985. Revision of *Taverniera* (Leguminosae-Papilionoideae). Symb. Bot. Upsal. **25**: 44–94.

Vogelsberger A. 1893. Ueber die systematische Bedeutung anatomischen charactere der Hedysareen. Ph.D. thesis. K.B. Friedrich-Alexander-Univesitat zu Erlangen, 59 pp.

Watari S. 1934. Anatomical studies on some Leguminous leaves with special reference to the vascular system in petioles and rachises. J. Fac. Sci., Imp. Univ. Tokyo, Sect. III (Botany) **4**: 225–365.

Wylie R. B. 1952. The bundle sheath extension in leaves of Dicotyledons. Amer. J. Bot. **39**: 645–651.

Appendix 1: List of specimens examined and their figure number illustrated.

1. Nodal region

***Hedysarum** coronarium* L. (subgenus Hedysarum): Italy, Sicily, 2 June 1979, P. Davis et al. 64330 (BM).

H. fruticosum subsp. *mongolium* Turcz. ex B.Fedtsch. (subgen. Heteroloma): China, Inner Mongolia, Damogi, Aguei, 23 Aug. 1975, Men Pu 305 (TUS), Fig. 4.

H. gmelini Ledeb. (subgen. Gamotion sect. Multicaulia): China, 1959, Mongmuxiuyuan 6 (TUS), Fig. 1.

H. membranaceum Coss. & Bal. (subgen. Gamotion sect. Membranacea): Moroco, 14 June 1980, J. Lewalle 9634 (BM).

H. monophyllum Boriss. (subgen. Gamotion sect. Subacaulia): Asia media, Pamiralaj, 28 June 1935, Dshanaera s.n. (E), Fig. 2.

H. spinosissimum L.(subgen. Hedysarum): Greece, Berghen s.n. (BM), Fig. 3.

H. vicioides Turcz. var. *japonicum* (B.Fedtsch.) B.H.Choi & H.Ohashi (subgen. Gamotion sect. Gamotion): Japan, Miyagi Pref., Mt. Zao, 28 July 1985, Choi 369 (TUS), Fig. 5.

***Stracheya** tibetica* Benth.: W. Nepal, 2 July 1963, Stainton 4389 (TI), Fig. 6.

***Taverniera** nummularia* DC.: Orientale, 1868, C. Haussknecht s.n. (BM), Fig. 7.

2. Petioles

***Corethrodendron** scoparium* Fischer & Basiner: China, Johol, 28 Sept. 1933, T. Nakai s.n. (TUS), Fig. 8F.

Hedysarum L.

Subgen. Gamotion

Sect. Crinifera

H. macranthum Freyn & Sint.: Transcaspica, Aschabad, 26 May 1900, P. Sintenis 392 (E).

H. micropterum Bunge: Transcaspica, Kisil Arwat, 1901, P. Sintenis 1804 (E).

Sect. Gamotion

H. falconeri Baker: Karakoram, 7 July 1939, B.S. Russell 1109 (TI), Fig. 8D.

H. hedysaroides (L.) Schinz & Thell.: Japan, Mt. Taisetsu, Aug. 1928, T. Nakai s.n. (TI).

H. inundatum Turcz.: China, Wutaishan, 27 June 1942, Takahashi 415 (TI).

H. sikkimense Benth. ex Baker: Lama Chungbu, Kanai et al. s.n. (TI).

H. vicioides Turcz. var. *japonicum* (B.Fedtsch.) B.H.Choi & H.Ohashi: Japan, Mt. Iide, 6–9 Aug. 1973, H. Ohba et al. s.n. (TUS), Fig. 8C.

Sect. Membranacea

H. membranaceum Coss. & Bal.: Moroco, 14 June 1980, J. Lewalle 9634 (BM).

Sect. Multicaulia

H. brachypterum Bunge: China, 23 Aug.1976, Liu 488 (TUS).

H. gmelini Ledeb.: China, Inner Mongolia, Damogi, Aguei, 1959, Mongmuxiuyuan 6 (TUS)

Sect. Subacaulia

H. ferganense Korsh.: Altai, 20 Aug. 1945, collector unknown (BM).

H. monophyllum Boriss.: Asia media, Pamiralaj, 28 June 1935, Dshanaera s.n. (E), Fig 8B.

Subgen. Hedysarum

H. coronarium L.: Italy, Sicily, 2 June 1979, P. Davis et al. 64330 (BM), Fig. 8E.

H. glomeratum F. Dietr.: Sardina, 4 Aug. 1973, C. J. Humphries & I. B. K. Richardson 135 (BM).

H. spinosissimum L.: Spain, Balearic Isl., 16 Apr. 1971, J. F. M. & M. J. Cannon 3978 (BM), Fig. 8A.

Subgen. Heteroloma

H. fruticosum Pall. subsp. *mongolicum* Turcz. ex B.Fedtsch.: China, 23 Aug. 1975, Men Pu 305 (TUS).

H. multijugum Maxim.: China, Kansu, June 1915, Parrer & Purdom 668 (TUS).

***Stracheya** tibetica* Benth.: W. Nepal, 2 July 1963, Stainton 4389 (TI).

***Taverniera** nummularia* DC.: Bagdad, Aucher-Eloy 1080 (BM).

3. Leaflet

***Corethrodendron** scoparium* Fisch. & Basiner: China, 28 Sept. 1933, T. Nakai et al. s.n. (TI), Fig. 20; Prov. Hsingan, 12 Aug. 1936, Kitagawa s.n. (TI); China, Tatsingshan, Liu 98 (PE).

Genus **Hedysarum** L.

Subgen. Gamotion

Sect. Crinifera

H. macranthum Freyn & Sint.: Transcaspica, P.

Sinteins 392 (E); Asia media, Gnerdillo 47 (E).

H. micropterum Bunge: Transcaspica, Kisil Arwat, Karakola, 1901, P. Sintenis 1804 (E); Freyn s.n. (E), Fig. 14.

Sect. Gamotion

H. alpinum L.: China, Werleurkakaju, Turzaninow s.n. (E); China, Hsinganling, 3 July 1915, K. Yamatusta 158 (TI); Dahuria, Karo s.n. (E); China, Hsinganling, 29 July 1930, Kitagawa s.n. (TI).

H. blepharopterum Hand.-Mazz.: China, S. W. Szechwan, June 1929, J. F. Rock 17670 (E).

H. campylocarpon H.Ohashi: Nepal, Langtang, 23 June 1949, O. Polunin 562 (TI).

H. fistulosum Hand.-Mazz.: China, Yunnan, Aug. 1918, G. Forrest 17621 (E).

H. hedysaroides (L.) Schinz & Thell.: Japan, Taisetu-san, Aug. 1928, T. Nakai s.n. (TI); Italy, Gardner 2654 (BM); Japan, Isl. Rebun, 28 July 1983, H. Takahashi 4316 (TUS); Japan, Mt. Rakkodake, 11 Aug. 1933, H. Hara 3731a (TI).

H. limitaneum Hand.-Mazz.: W. China, 27 June 1913, F. Kingdon-Ward 584 (E).

H. limprichtii Ulbr.: China, Szechuan, R. Cunningham 186 (E).

H. manaslense H.Ohashi: Nepal, Bimtakothi, Lowndes 1474 (BM).

H. manaslense var. *nepalense* H.Ohashi: Nepal, Taglung, 11 July 1954, Stainton et al. 1698 (TI).

H. pseudoastragalus Ulbr.: W. China, 1911, F. Kingdon-Ward 175 (E); China, July 1921, G. Forrest 19612 (E).

H. semenowii Regel & Herder: Kazachstania, 10 July 1964, I. Roldugins s.n. (E).

H. sikkimense Benth. ex Baker var. *sikkimense*: E. Nepal, Kanai et al. 720706 (TI); Yunnan, F. Kingdon-Ward 4392 (E); Lichiang Range, G. Forrest 6210 (E); Arun Valley, Stainton 630 (TI); Butan, Ludlow et al. 20435 (TI); N. W. Yunnan and Tibet, F. Kingdon-Ward 983 (E).

H. sikkimense var. *megalanthum* H.Ohashi & Tateishi: W. China, 22 July 1913, F. Kingdon-Ward 858 (E), Fig. 13; S.E. Tibet, Ludlow et al. 13160 (E & TI); E. Tibet, J. F. Rock 14382 (E).

H. taoriparium B.H.Choi & H.Ohashi: China, Kansu, T'ao River basin, 6 July 1925, J. F. Rock 12623 (E-Holotype).

H. tuberosum B.Fedtsch.: China, Kansu, July, R. Farrer & W. Purdom 105 (E).

H. vicioides Turcz var. *chinense* B.H.Choi & H.Ohashi: China, Mts. Tatsingshan, Ma et al. 7 (TUS).

H. vicioides var. *japonicum* (B.Fedtsch.) B.H.Choi & H.Ohashi: Cultivated at the green house of Tohoku Univ., original plant collected by Ohba s.n., Aug. 1973, Fig. 9; Japan, Mt. Zao, 28 July 1985, Choi 369 (TUS); Japan, Mt. Iide, H. Ohba et al. s.n. (TUS); Japan, Mt. Yukikuradake, H. Sakai 840392 (TUS).

Sect. Membranacea

H. membranaceum Coss. & Bal.: Moroco, 20 Aug. 1968, Goodchild 62 (BM); Lewalle 9634 (BM), Fig. 17.

Sect. Multicaulia

H. cephalotes Franch.: Chitral, J.D.A. Stainton 2631 (BM).

H. ferganense Korsh.: Kirghizia, 30 June 1968, B. Saltanova s.n. (E), Fig. 11.

H. gmelini Ledeb.: Altai, 22 July 1930, P. Smirnow s.n. (E); China, Inner Mongolia, Damogi, Aguei, 1959, Mongmuxiuyuan 6 (TUS).

H. iomuticum B.Fedtsch.: USSR, Uzbekistania, date unknown, V. Botschantzev & A. Vvedensky s.n. (E).

H. jaxarticum Popov.: USSR, Kazachstania, date unknown, S. Granitov s.n. (E).

H. kumaonense Benth. ex Baker: Nepal, date unknown, Stainton 856 (TI); Nepal, Polunin 2182 (TI).

H. lehmannianum Bunge: Asia media, Pamiralaj, 28 July 1930, Pazij & Uironov s.n. (E), Fig. 16.

H. songolicum Bongard: USSR, Kazachstania, 25 June 1959, V. Goloskokov s.n. (E).

H. subglabrum (Kar. & Kir.) B.Fedtsch.: locality and date unknown, Goloskokov s.n. (E), Fig. 15.

Sect. Subacaulia

H. monophyllum Boriss.: Asia media, Pamiralaj, 28 July 1935, Dshanaera s.n. (E); Turcomania, D. Litwinow 628 (E).

H. splendens Fisch.ex DC.: Songaria, Chin ad locum Saisang-Nor., coll. unknown (E).

Subgen. Hedysarum

H. coronarium L.: Cultivated at the green house of Tohoku Univ., 1985, original collecting data unknown, Figs. 10, 12, 18; Spain, Cadiz, 27 April 1961, C. A. Walker 95 (BM); Siciley, 2 June 1979, P. Davis & D. S. Sutton 64330 (BM).

H. glomeratum F.Dietr.: Spain, Andalucia, D. Brinton-Lee 1135 (BM); Sardinia, Capo Figara, 8 Apr. 1973, C. J. Humphrico & I. B. K. Richardson 135 (BM).

H. spinosissimum L.: Greece, C.V. Berghen s.n. (BM); Spain, Baleares, 15 Apr. 1971, J. F. M. & M. J. Cannon 3978 (BM); Spain, Prov. Almeria, 12 Apr. 1982, M. F. & S. G. Gardner 1592 (BM).

Subgen. Heteroloma

H. fruticosum Pall. subsp. *mongolicum* Turcz. ex B.Fedtsch.: China, Men-Pu 305 (TUS); Mongolia, 12 Aug. 1943, Togashi s.n. (TI); Hokushi Keihosen, M. Togashi 727 (TI), Fig. 19; Sibiria, coll. unknown (E); Mongolia Occidentalis, 1871, N. M. Przewalski s.n. (E).

H. multijugum Maxim.: E. Tibet, July 1926, J. F. Rock 14363 (E); China, Kansu, Parrer & Purdom 668 (TUS); China, Kansu, Umemura 19 (TI); Mongolia, coll. unknown (E).

Stracheya ***tibetica*** Benth.: S. Tibet, N. Humphreys 5040 (TI), Fig. 22; Tibet, date unknown, E. Kawaguchi s.n. (TI); Dolpo, 2 July 1963, J.B.A. Stainton 4389 (TI).

Taverniera nummularia DC.: Orientale, 1868, Haussknesht s.n. (BM), Fig. 21.

崔 秉熙[a]，根本智行[b,*]，大橋広好[b]：**マメ科イワオウギ属と近縁属における節と葉の解剖学的研究**

イワオウギ属と近縁の *Corethrodendron* 属，*Stracheya* 属および *Taverniera* 属では，属の範囲の設定に見解の相違がある．これらの分類群では，托葉の形態，小葉数および小葉表面の形状に変異がみられることから，節から葉柄中部までの維管束走行および葉の解剖学的特徴と表皮形態について，属間およびイワオウギ属の属内分類群間で比較し，各分類群間の類縁関係を検討した．

節部の葉隙には三隙型と多隙型の2型がみられた．節部の中心柱より分岐した中央と側方の葉跡は，葉柄の基部あるいは中央付近で離生するものから融合あるいは合着するものまで変異がみられた．さらに，葉柄中央付近の維管束走行には維管束の配置や本数および中央維管束や向軸側維管束の有無によって6タイプを認めた．イワオウギ属には托葉が葉柄基部に合着するものと離生するものがあるが，この形質と関連する維管束走行パターンはみられなかった．また，小葉数の変異と関連する維管束走行パターンもみられなかった．

また，葉の解剖学的特徴および表皮形態の比較の結果，維管束鞘の有無とクチクラ層の発達の程度に分類群間で変異がみられた．維管束鞘はイワオウギ属 Gamotion 亜属 Gamotion 節にのみみられた．

本研究の結果，イワオウギ属 Gamotion 亜属は *Stracheya* 属と節および葉の解剖学的特徴で類似すること，また，イワオウギ属 Heteroloma 亜属は *Corethrodendron* 属，*Taverniera* 属と節解剖，葉跡および葉の表皮の特徴で類似することが明かとなり，これらの分類群間の関係は花粉形態の結果（Choi and Ohashi 1996）と一致した．

（[a]仁荷大学校理科大学生物学科，
[b]東北大学大学院理学研究科生物学専攻，
[*]現住所：石巻専修大学理工学部基礎理学科）